Evaluation of Potato Clones for Severity of Verticillium Wilt, Yield and Specific Gravity in Maine

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ABSTRACT

In 1994 and 1995, the effect of Verticillium wilt, caused by *Verticillium dahliae* and *V. albo-atrum*, on tuber yields, number and weight of U.S. No. 1 and B size tubers, and specific gravity was studied in northern Maine, an area with a short growing season. Seven clones (four resistant and three susceptible) were evaluated in a split-plot design with three replications. Clones were the whole-plot factor, and seed pieces in sub-plots were either uninoculated or inoculated with 50 ml of 4 x 10^4 cfu/ml *Verticillium* spp. at planting. Individual plants were scored for Verticillium wilt symptoms before harvest on a 1= <3% wilt to 10= >97% wilt. Differences among clones for wilting and specific gravity were significant. The inoculation treatment had no effect on any of the tuber traits measured. However, there were significant clone x inoculation interactions for most tuber traits. Reductions in yield, weight and number of U.S. No. 1 potatoes, and specific gravity were greater in the Verticillium wilt susceptible clones than in the resistant clones. These results suggest that breeding clones with resistance to *Verticillium* spp. will reduce yield losses, while maintaining tuber size and specific gravity under disease pressure.

INTRODUCTION

Verticillium albo-atrum Reinke & Berthier and *V. dahliae* Kleb. are fungal pathogens that cause Verticillium wilt of many plant species, including potato (*Solanum tuberosum* L.) (Rowe *et al.*, 1987). *Verticillium dahliae* predominates in potato growing areas where average ambient summer air temperatures frequently exceed 25 C, particularly in the North Central states and the Pacific Northwest in the U.S. (Powelson and Rowe, 1993). Both *V. dahliae* and *V. albo-atrum* occur in cooler production areas of the United States, such as Maine, the Red River Valley, and the winter production areas of Florida (Powelson and Rowe, 1993).

Symptoms of plants infected by these pathogens are recoverable true wilting, unilateral permanent wilting, unilateral chlorosis, and necrosis (Isaac and Harrison, 1968). Another symptom is premature maturation or senescence, commonly called potato early dying (Isaac and Harrison, 1968).

Yield losses due to Verticillium wilt of up to 50% have been reported (Rowe *et al.*, 1987). Although soil type does not affect yield reductions caused by infections with *V. dahliae* (Francl *et al.*, 1988), increased levels of Verticillium wilt have been associated with excessive irrigation or wet growing seasons (Davis *et al.*, 1990; Cappaert *et al.*, 1992). Nitrogen deficiency has increased the severity of Verticillium wilt (Davis and Everson, 1986). Using the susceptible cultivar Superior in microplot studies, Botseas and Rowe (1994) found a significant increase in the number of tubers less than 6.4 and between 6.4 and 8.3 cm in diameter in *V. dahliae* infested soil than in non-infested soil. Although they found no significant difference in total yield between the *V. dahliae* infested and non-infested soil, they concluded that size differences may reduce marketable yields.

In addition to affecting yield and tuber size distribution, Verticillium wilt affects other important quality factors in potatoes. Davis *et al.* (1995) reported a negative correlation between *V. dahliae* in root infections and specific gravity in the cv Russet Burbank. Cole *et al.* (1972) reported that *V. albo-atrum* caused stem end discoloration in tubers of

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Katahdin and Kennebec. An association between Verticillium and the pink-eye disease has also been reported (Cole *et al.*, 1972; Goth *et al.*, 1993). However, this association may be the result of the particular clones investigated, since further studies found that resistance to Verticillium wilt and pink-eye disease segregate independently (Goth *et al.*, 1994).

Integrated crop management systems are necessary to limit the losses caused by Verticillium wilt (Powelson and Rowe, 1993). Soil fumigation, cultural methods, and host resistance are the three major components of these integrated systems. Much of the research on the effect of Verticillium wilt on yield, tuber size distribution, and specific gravity has been conducted on Russet Burbank, an economically important cultivar widely grown in the Pacific Northwest and other areas where *V. dahliae* predominates. The results of these studies are often based on survey data and reported reductions in yields are confounded with location and/or year effects that cannot be measured. Other studies have used controlled conditions in micro-plots to compensate for this confounding effect, but how these relate to the field situation is a major concern (Jeger *et al.*, 1996). Therefore, studies on the effect of Verticillium wilt on yield, tuber size distribution, and specific gravity of potatoes from diverse genetic backgrounds grown under a range of environments and pathogens are warranted. The information derived from these studies would be useful in developing Verticillium wilt resistant cultivars and improving integrated biological control methods.

The objectives of this study were to evaluate the effect of *Verticillium* spp. on yield, tuber size distribution, and specific gravity in seven potato clones representing a range of reactions to Verticillium wilt in northern Maine.

MATERIALS AND METHODS

Isolates of *V. albo-atrum* and V. *dahliae* recovered from potato stems with early dying symptoms in 1993 and 1994 and stored on Difco potato dextrose agar at 20-24 C were used in this study. The inoculum was prepared by streaking conidial suspensions of the test isolates onto prune extract agar (Talboys, 1960). After 10-20 days, the prune extract agar and the resultant growth were mixed volume/volume with distilled water and comminuted with a blender. Inoculum consisted of approximately equal amounts of *V. albo-atrum* and *V. dahliae*. Distilled water was used to dilute the resultant slurry to a concentration of 4×10^4 cfu per ml.

Four cultivars and three breeding selections (clones) were used in this study. Abnaki, B0169-56, Reddale, and Russette, are known to be resistant to Verticillium wilt; B0178-35, B0233-1, and Superior are known to be susceptible (Goth *et al.*, 1993).

The experimental design was a split-plot with three replications. Clones were the whole-plot factor, and sub-plots were either uninoculated or inoculated with *Verticillium* spp. Each sub-plot consisted of five rows of ten plants per row. Plants were spaced 30 cm within the row, in rows 91 cm apart. Field plots at the Aroostook State Farm, Presque Isle, ME were planted on 15 June 1994 and 9 June 1995, on a Caribou silt loam soil which was in an oat-potato rotation. Each seed tuber was cut into seed pieces weighing 40-60 g, and seed pieces in the inoculated sub-plots were immersed in the inoculum and hand planted in row. Immediately after planting, an additional 50 ml of the inoculum was poured over the seed pieces, and the seed pieces were covered with approximately 15 cm of soil. Uninoculated seed pieces were treated in a similar manner, but without inoculum.

Plots were fertilized with 14-14-14 NPK at 1100 kg/ha. Weeds and grasses were controlled with Lorox (linuron) 0.6 kg a.i./ha and Poast (sethoxydim) 0.3 kg a.i./ha. Other standard recommended spray and cropping practices were followed during the growing season. Irrigation was not available.

On 31 August 1994 and 22 August 1995, 77 and 74 days after planting (DAP), respectively, every plant in each plot was rated for severity of wilt on a modified Horsfall-Barratt scale (Horsfall and Barratt, 1945), where 1=0-3%, 2=3-6%, 3=6-12%, 4=12-25%, 5=25-50%, 6=50-75%, 7=75-87%, 8=87-93%, 9=93-97%, and 10=97-100% wilt. An average of these ratings for each sub-plot was computed. Immediately after scoring for wilt, selected stem samples of plants without symptoms and those with representative infections were assayed for the presence of *Verticillium* spp. (Goth *et al.*, 1993). Vines were mechanically removed with a rotobeater immediately prior to harvest.

Tubers were harvested on 21 September 1994 and 25 September 1995, 98 and 109 DAP, respectively. The number and yield of potatoes <4.8 cm and >4.8 cm in diameter were recorded. Specific gravity was determined by the weight in air and weight in water method (Murphy and Goven, 1959) within a month of harvest.

All variables were analyzed using the general linear models procedure in the Statistical Analysis System (SAS, 1987). All effects were considered random except the inoculated vs. uninoculated effect (denoted inoc). Where appropriate (*i.e.* when variances for a given trait in 1994 and 1995 were homogeneous) the data were combined over years for analysis.

Satterwaite's approximation (Satterwaite, 1946) was used to test the inoculation effect as $MS_i/(MS_{yi} + MS_{ci} - MS_e)$; to test the clone effect as $MS_c/(MS_{yc} + MS_{yci} - MS_e)$; and to test the rep (year) effect as $MS_{r(y)}/(MS_{cr(y)} + MS_{ir(y)} - MS_e)$, where MS=mean squares and the subscripts refer to y=year, r=replication, c=clone, i=inoculation, and e=error. Least square means were calculated for total yield, weight and number of US No. 1 and B size potatoes, and specific gravity (SAS, 1987).

RESULTS AND DISCUSSION

V. albo-atrum and *V. dahliae* were only recovered from stems of inoculated plants. This suggests that the symptoms and concomitant wilt results were caused by infection by these *Verticillium* species. Thus, the field plot used in this experiment provided a unique opportunity to evaluate the effect of *Verticillium* spp. on yield, tuber size distribution and specific gravity in potatoes without the confounding effects of years and locations present in previously reported survey data.

As expected, there were significant differences among clones and the inoculated vs. uninoculated effects and the clone x inoculation interaction effects were also significant for average Verticillium wilt rating (Table 1). In agreement with previous findings (Goth *et al.*,1993), Abnaki, B0169-56, Reddale, and Russette were resistant, and B0178-35, B0233-1, and Superior were susceptible (Table 2). The average amount of wilt in the resistant clones was less than 6%, whereas, the average amount of wilt in the susceptible clones was greater than 25%. The average wilt rating in the inoculated plots was higher in 1994 (3.95) than in 1995 (3.36), whereas, the average wilt ratings were similar in the uninoculated plots both years (1.21 vs. 1.24). There was significantly more variation for wilt in 1994 (0.48) than in 1995 (0.14) ($F=3.43$, $P<0.05$). This would be expected when environmental conditions were more conducive to Verticillium wilt in one year than another. Rainfall during the 1994 growing season was higher than normal (35 cm vs. 29 cm), even though little rain fell during August (3.2 cm). Rainfall during the 1995 growing season was approximately half of normal (16 cm vs. 29 cm), which may explain the lower wilt ratings. Verticillium wilt has been reported to be more severe during wet growing seasons than during dry growing seasons (Davis *et al.*, 1990; Cappaert *et al.*, 1992).

The clone x year, inoculation x year, and clone x inoculation interaction effects were all significant for total yield (Table 3). Overall, yields were reduced 28.5% in inoculated plots in 1994 and only 7% in inoculated plots in 1995 (Table 4). The greatest reductions in yield occurred in the susceptible

TABLE 1.—*Mean squares from the analysis of variance on the average Verticillium wilt rating*[a] *of potato clones in the Verticillium wilt study conducted in 1994 and 1995 in Presque Isle, Maine.*

		Mean Squares	
Source	d.f.	1994	1995
Rep	2	0.48	0.18
Clone	6	5.63**	5.86**
Error a	12	0.66	0.46*
Inoc	1	78.69**	47.10**
Clone x inoc	6	4.20**	3.29**
Error b	14	0.48	0.14
Total	41		

*,** Significant at the 5% and 1% level, respectively.
[a]Verticillium wilt was scored on a scale of 1= <3% to 10= >97% wilt. Average Verticillium wilt rating based on individual ratings of 50 plants per sub-plot.

TABLE 2.—*Average Verticillium wilt rating*[a] *of potato clones in the Verticillium wilt study conducted in 1994 and 1995 in Presque Isle, Maine.*

		Verticillium Wilt	
Clone	Inoculation[b]	1994	1995
Abnaki	I	2.37	2.44
	U	1.17	1.09
B0169-56	I	2.79	1.39
	U	1.13	1.00
Reddale	I	2.23	2.43
	U	1.07	1.45
Russette	I	2.74	2.37
	U	1.05	1.01
B0178-35	I	6.28	4.77
	U	1.18	1.00
B0233-1	I	5.39	3.79
	U	1.26	1.11
Superior	I	5.86	6.31
	U	1.65	2.03
Resistant	I	2.53	2.16
Clones	U	1.11	1.14
Susceptible	I	5.84	4.96
Clones	U	1.36	1.38
Overall	I	3.95	3.36
	U	1.21	1.24

[a]Verticillium wilt was scored on a scale of 1= <3% to 10= > 97% wilt. Average Verticillium wilt rating based on individual ratings of 50 plants per sub-plot.
[b]I= Sub-plots inoculated with 50 ml of 4×10^4 cfu/ml of *Verticillium albo-atrum* and *V. dahliae*. U = uninoculated sub-plots.

Table 3.—*Mean squares from the analyses of variance on total yield, weight of US No. 1 and weight of B size tubers harvested from the Verticillium wilt study conducted in 1994 and 1995 in Presque Isle, ME.*

		Mean Squares		
Source	d.f.	Total Yield	Weight US No.1	Weight B size
Year	1	738.6	431.7	17.32*
Rep (year)	4	192.7*	206.9**	2.06*
Clone	6	406.9	406.7	10.28
Clone x year	6	147.2**	126.2**	2.94**
Clone x rep (year)	24	18.3	19.3	0.42
Inoc	1	970.2	1213.0	15.86
Inoc x year	1	446.1**	469.7**	0.73
Inoc x rep (year)	4	6.3	6.8	0.16
Clone x inoc	6	104.6*	109.7*	1.05*
Year x clone x inoc	6	17.6	15.3	0.21
Error	24	15.4	14.9	0.36
Total	83			

*,** Significant at the 5% and 1% levels, respectively.

TABLE 4.—*Effect of inoculation with* Verticillium albo-atrum *and* V. dahliae *on total yield (kg/sub-plot) and weight of US No. 1 and B size tubers (kg/sub-plot) in the Verticillium wilt study conducted in 1994 and 1995 in Presque Isle, Maine.*

		Total Yield[a]		Weight US No. 1[a]		Weight B Size[a]	
Clone	Inoculation[b]	1994	1995	1994	1995	1994	1995
Abnaki	I	33.9	30.3	30.3	27.1	3.1	3.2
	U	43.4	30.5	39.6	27.3	3.2	3.2
B0169-56	I	38.3	26.5	31.2	22.8	6.7	3.7
	U	44.3	22.2	39.1	19.4	4.8	2.8
Reddale	I	45.7	36.6	42.1	35.0	3.0	1.6
	U	47.4	35.2	44.6	33.5	2.4	1.7
Russette	I	31.4	28.8	27.0	25.9	3.8	2.9
	U	36.0	30.5	33.0	28.1	2.7	2.5
B0178-35	I	23.0	23.8	17.0	20.3	5.6	3.5
	U	40.8	28.5	35.9	26.2	3.9	2.4
B0233-1	I	16.6	24.0	14.1	21.5	2.4	2.5
	U	37.6	29.0	35.9	27.3	1.2	1.7
Superior	I	11.2	20.9	7.6	18.1	3.3	2.8
	U	30.4	30.2	27.4	28.9	2.3	1.3
Resistant	I	37.3	30.6	32.7	27.7	4.2	2.9
Clones	U	42.8	29.6	39.1	27.1	3.3	2.6
Susceptible	I	16.9	22.9	12.9	20.0	3.8	2.9
Clones	U	36.3	29.2	33.1	27.5	2.5	1.8
Overall	I	28.6	27.3	24.2	24.4	4.0	2.9
	U	40.0	29.5	36.5	27.2	2.9	2.2

[a]Least square means given for all variables.
[b]I= Sub-plots inoculated with 50 ml of 4 x 10^4 cfu/ml of *Verticillium albo-atrum* and *V. dahliae*. U = uninoculated sub-plots.

clones. In 1994 and 1995, yields were reduced an average of 53% and 22% in susceptible clones, respectively. In contrast, yields were reduced 13% in 1994 and yields actually increased 3% in 1995 in the resistant clones. Thus, greater reductions in yield were associated with a higher degree of wilting due to Verticillium infection.

The clone x year, inoculation x year, and clone x inoculation interaction effects were all significant for weight of US No. 1 potatoes (Table 3). Overall, the weight of US No. 1 potatoes was reduced 33.7% in the inoculated plots in 1994 and only 10.3% in inoculated plots in 1995 (Table 4). The greatest reductions in weight of US No. 1 potatoes occurred in the susceptible clones. In 1994 and 1995 the weight of US No. 1 potatoes was reduced an average of 61.0% and 27.3% in the susceptible clones, respectively. In contrast, the weight of US No. 1 potatoes was reduced 16% in 1994 and increased 2.2% in 1995 in the resistant clones.

There was a significant difference between years for weight of B size potatoes, and the clone x year, and clone x inoculation interaction effects were also significant (Table 3). The weight of B size potatoes was greater in 1994 than in 1995 (Table 4). Overall, the weight of B size potatoes increased 37.9% and 31.8% in inoculated plots in 1994 and 1995, respectively. The largest increase in the weight of B size potatoes occurred in the susceptible clones. In 1994 and 1995, the weight of B size potatoes increased an average of 52.0% and 61.1% in the susceptible clones, respectively. In contrast, the weight of B size potatoes only increased an average of 27.3% and 11.5% in the resistant clones in 1994 and 1995, respectively.

The clone x year, inoculation x year, and clone x inoculation interaction effects were significant for the number of US No. 1 potatoes (Table 5). Overall, the number of US No. 1 potatoes decreased by 22.9% and 11.2% in the inoculated plots in 1994 and 1995, respectively, as compared to the uninoculated plots (Table 6). The largest decrease in the number of US No. 1 potatoes occurred in the susceptible clones. In 1994 and 1995 the four resistant clones produced 8.5% less and 0.6% more US No. 1 tubers, respectively, in the inoculated plots than in the uninoculated plots, whereas, the three susceptible clones produced 44.2% and 27.3% less US No. 1 tubers, respectively, in the inoculated plots than in the uninoculated plots. A bigger decrease in the number of US No. 1 potatoes was associated with a higher degree of wilting due to Verticillium infection.

There was a significant difference between years for the number of B size potatoes, and the clone x year interaction effect was significant (Table 5). More B size potatoes were

TABLE 5.—*Mean squares from the analyses of variance on number of US No. 1 tubers, number of B size tubers, and specific gravity of tubers harvested from the Verticillium wilt study conducted in 1994 and 1995 in Presque, Isle, ME.*

		Mean Squares		
Source	d.f.	Number US No.1	Number B size	Specific Gravity
Year	1	7012	27008*	78.59
Rep (year)	4	3331*	1476*	37.26*
Clone	6	6318	6609	574.26**
Clone x year	6	3312**	1893**	61.44**
Clone x rep (year)	24	377	302	4.61
Inoc	1	20305	8731	174.73
Inoc x year	1	3487*	303	10.47
Inoc x rep (year)	4	396	61	6.11
Clone x inoc	6	3375**	539	55.64**
Year x clone x inoc	6	189	191	2.04
Error	24	365	224	3.57
Total	83			

*,** Significant at the 5% and 1% levels, respectively.

TABLE 6.—*Effect of inoculation with* Verticillium albo-atrum *and* V. dahliae *on the number of US No. l and B size tubers, and specific gravity in the Verticillium wilt study conducted in 1994 and 1995 in Presque Isle, Maine.*

		Number US No.1[a,b]		Number B Size[a,b]		Specific Gravity[a]	
Clone	Inoculation[c]	1994	1995	1994	1995	1994	1995
Abnaki	I	176	172	93	85	1.075	1.075
	U	195	176	97	75	1.074	1.074
B0169-56	I	206	138	163	78	1.086	1.077
	U	232	125	118	63	1.085	1.076
Reddale	I	194	168	83	42	1.069	1.071
	U	189	167	74	39	1.069	1.072
Russette	I	158	169	97	56	1.090	1.084
	U	187	177	75	46	1.093	1.085
B0178-35	I	138	137	158	81	1.088	1.088
	U	208	167	105	55	1.091	1.089
B0233-1	I	98	126	52	53	1.073	1.073
	U	156	151	31	34	1.081	1.077
Superior	I	67	89	86	58	1.071	1.076
	U	178	165	62	27	1.084	1.086
Resistant	I	184	162	109	65	1.080	1.077
Clones	U	201	161	91	56	1.080	1.077
Susceptible	I	101	117	99	64	1.077	1.079
Clones	U	181	161	66	39	1.085	1.084
Overall	I	148	143	105	65	1.078	1.078
	U	192	161	80	48	1.082	1.080

[a]Least square means given for all variables.
[b]Total number of tubers per 50 hill sub-plot.
[c]I= Sub-plots inoculated with 50 ml of 4 x 10^4 cfu/ml of *Verticillium albo-atrum* and *V. dahliae*. U = uninoculated sub-plots.

produced in 1994 than in 1995 (Table 6). The susceptible clones produced 50% and 64% more B size potatoes in the inoculated plots than in the uninoculated plots in 1994 and 1995, respectively. The resistant clones produced 20% and 16% more B size potatoes in the inoculated plots than in the uninoculated plots in 1994 and 1995, respectively. Thus, a large increase in the number of B size potatoes was associated with clonal susceptibility to *Verticillium* infection.

There were significant differences among clones for specfic gravity (Table 5). The specific gravities of B0178-35 and Russette were high; Abnaki and Reddale were low; and B0169-56, B0233-1, and Superior were intermediate (Table 6). The clone x inoculation interaction was also significant. In general, there was a significant decrease in specific gravity for susceptible clones in the inoculated plots as compared to the uninoculated plots. The mean decrease in specific gravity for susceptible clones in the inoculated plots as compared to the uninoculated plots was 0.0065. There was no significant decrease in specific gravity for resistant clones in the inoculated plots as compared to the uninoculated plots. There was no discernable relationship between specific gravity and resistance to Verticillium wilt in this study. For the two high specific gravity clones, one (B0178-35) was susceptible Verticillium wilt and one (Russette) was resistant. Among the three intermediate specific gravity clones, B0169-56 was resistant, while B0233-1 and Superior were susceptible. These results suggest that the development of clones with resistance to Verticillium wilt will help those clones to maintain their specific gravity under disease pressure from *Verticillium* spp. This will be especially important in the development of clones for the french fry and chipping industries where high specific gravity tubers are preferred.

The results of this study conclusively demonstrate the adverse effect of Verticillium wilt on total yield, tuber size distribution and specific gravity in Verticillium susceptible clones. The effect of Verticillium wilt on total yield, number and weight of US No. 1 and B size tubers, and specific gravity in resistant potato clones is much less than in susceptible clones suggesting that the development of commercially acceptable potato cultivars with high levels of resistance to Verticillium will allow growers to produce and market their crop while minimizing the negative impact of infection by *Verticillium* spp. on economically important traits such as yield, size distribution, and specific gravity. In addition to this immediate benefit, Davis *et al.* (1994) have shown that inoculum densities of *V. dahliae* in the soil can be reduced by growing resistant cultivars to the point where the severity of Verticillium wilt is limited in subsequent years even when a susceptible cultivar is planted. Thus, the development of Verticillium wilt resistant cultivars has an important part to play in managing this disease in an environmentally sound way.

LITERATURE CITED

Botseas, D.D. and R.C. Rowe. 1994. Development of potato early dying in response to infection by two pathotypes of *Verticillium dahliae* and co-infection by *Pratylenchus penetrans*. Phytopathology 84:275-282.

Cappaert, M.R., M.L. Powelson, N.W. Christensen, and F.J. Crowe. 1992. Influence of irrigation on severity of potato early dying and tuber yield. Phytopathology 82:1448-1453.

Cole, H., W.R. Mills, and L.B. Massie. 1972. Influence of chemical seed and soil treatments on *Verticillium*-induced yield reduction and tuber defects. Am Potato J 49:79-92.

Davis, J.R. and D.O. Everson. 1986. Relation of *Verticillium dahliae* in soil and potato tissue, irrigation methods, and N-fertility to Verticillium wilt of potato. Phytopathology 76:730-736.

Davis, J.R., O.C. Huisman, L.H. Sorensen, and A.T. Schneider. 1995. Verticillium dahliae: a key factor influencing specific gravity and production of the Russet Burbank potato. Am Potato J 72:618.

Davis, J.R., J.J. Pavek, D.L. Corsini, L.H. Sorenson, A.T. Schneider, D.O. Overson, D.T. Westermann, and O.C. Huisman. 1994. Influence of continuous cropping of several potato clones on the epidemiology of Verticillium wilt of potato. Phytopathology 84:207-214.

Davis, J.R., L.H. Sorenson, J.C. Stark, and D.T. Westermann. 1990. Fertility and management practices to control verticillium wilt of the Russet Burbank potato. Am Potato J 67:55-65.

Francl, L.J., R.C. Rowe, R.M. Riedel, and L.V. Madden. 1988. Effects of three soil types on potato early dying disease and associated yield reduction. Phytopathology 78:159-166.

Goth, R.W., K.G. Haynes, and D.R. Wilson. 1993. Relationship of Verticillium wilt with pink-eye of potato in Maine. Plant Disease 77:402-405.

Goth, R.W., K.G. Haynes, and D.R. Wilson. 1994. Independent segregation in potato for resistance to Verticillium wilt and pink-eye. Plant Disease 78:562-564.

Horsfall, J.G. and R.W. Barratt. 1945. An improved grading system for measuring plant diseases. Phytopathology 35:655.

Isaac, I. and J.A.C. Harrison. 1968. The symptoms and causal agents of early dying (Verticillium wilt) of potatoes. Ann Appl Biol 61:231-244.

Jeger, M.J., G.A. Hide, P.H.J.F. Van den Boogert, A.J. Termorshuizen, and P. Van Baarlen. 1996. Pathology and control of soil-borne fungal pathogens of potato. Potato Research 39:437-469.

Murphy, H.J. and M.J. Goven. 1959. Factors affecting the specific gravity of the white potato. Maine Agri Exp Sta Bull 583:24p.

Powelson, M.L. and R.C. Rowe. 1993. Biology and management of early dying of potatoes. Ann Review Phytopathology 31:111-126.

Rowe, R.C., J.R. Davis, M.L. Powelson, and D.I. Rouse. 1987. Potato early dying: causal agents and management. Plant Disease 71:482-489.

SAS Institute. 1987. SAS/STAT guide for personal computers. Version 6 ed. SAS Inst., Inc., Cary, NC.

Satterwaite, F.E. 1946. An approximate distribution of estimates of variance components. Biometrics Bull 2:110-114.

Talboys, P.W. 1960. A culture medium aiding in the identification of *Verticillium albo-atrum* and *V. dahliae*. Plant Pathol 9:57-58.